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Metameric Color Pattern in the Bugs (Heteroptera: Lygaeidae, Largidae, Pyrrhocoridae, Rhopalidae): A Morphological Marker of Insect Body Compartmentalization

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ABSTRACT—Diversity of abdominal color patterns in some coreoid bugs (Heteroptera: Pentatomomorpha: Lygaeidae, Largidae, Pyrrhocoridae, Rhopalidae) is used as a morphological marker to reveal the developmental organization of the abdominal segments. Dominant metameric arrangement of these color patterns is documented by comparison of 160 species, and those results are supplemented by detailed analysis of two model species (*Pyrrhocoris apterus, Dysdercus cingulatus*), including a preliminary clonal analysis of mosaic epidermis in the *P. apterus* mutant strain. This allows the conclusion that (a) the intrasegemental transversal line, marked by contrasting epidermal coloration in the model species, has some properties of the intrasegmental compartmental boundary known in the *Drosophila* segments; (b) this boundary has a considerable role in cuticular color-pattern formation, being hardly exceedable for the cuticular spots established in one half of the segment; and (c) a great majority of the cuticular color patterns, although polyphyletically evolved, follows the same organizational scheme, and their diversity can thus be regarded as constrained by the compartmental boundaries.

INTRODUCTION

The segmentation of the insect body during development have been studied predominantly in *Drosophila,* a species possessing an extremely advanced body plan (for reviews see [1, 6, 8, 14, 18, 25]). The use of *Drosophila* as a model allows us to employ the latest methodologies of molecular genetics and developmental biology. Yet many findings derived from *Drosophila* may pertain only to cyclorrhaphous flies, and may not be sufficient for a general scheme of the insect (or even arthropod and articulate) body plan. A broader comparative survey of the segmentation processes in other insects or arthropods is therefore required. Sander [23] considers spontaneous or experimentally-induced teratological "monsters" a basis for ontogenetic analyses of arthropods which are still unapproachable by genetic methods (i.e., a vast majority of cases). We believe, however, that phylogenetic studies of diversity patterns can also provide a similarly valuable source of evidence.

The studies of Minelli and Bortoletto [19], Emerson and Schram [3], and Nijhout [21] are of particular interest in this respect. These studies deal primarily with morphology rather than genetics or developmental biology, proceeding by three principal steps: (1) description of the diversity pattern, (2) determination of the regularities involved in this diversity, and (3) confrontation of these pattern regularities with presumably relevant developmental processes. The discovery of a convenient morphological trait that would serve as a marker of the sought developmental rules is the critical point in this approach.

Cuticular coloration of some bugs belonging to the superfamily Coreoidea s. lat. (Pentatomonorpha; [24, 29] and references therein) displays conspicuous red-, ochre- or orange-and-black wasp-like patterns on the abdominal segments. The light (non-melanized) and dark (melanized) halves of the individual segments usually alternate regularly. This "half-segment" arrangement of the color pat-

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tern is interesting in terms of the anterior-posterior pattern-formation of the insect body. The coreoid bugs should therefore provide a good model group for developmental studies.

In the present paper, we attempt to examine the color patterns in a variety of species (160 spp.). The results are supplemented by more detailed analysis of the model species [*Pyrrhocoris apterus* (Linnaeus, 1758), *Dysdercus cingulatus* (Fabricius, 1775); both Pyrrhocoridae], including a preliminary clonal analysis of the epidermis in the *P. apterus* mutant strain *mosaic* (*mo*) [20, 26–27].

MATERIALS AND METHODS

Material

The insects used for comparative studies were obtained from the American Museum of Natural History (New York), National Museum (Praha), Moravian Land Museum (Brno), University of Connecticut (Storrs), and Charles University (Praha).

160 species of five higher taxa of the Coreoidea s. lat., viz. Lygaeinae (Lygaeidae: 34 species), Rhyparochrominae (Lygaeidae: 43 spp.), Largidae (9 spp.), Pyrrhocoridae (57 spp.) and Rhopalidae (17 spp.), were examined. Unless otherwise stated, only the adults were studied. Individual variability and sexual dichroism were tentatively checked in approximately 35% of the examined species and found negligible; therefore they were omitted from further analysis.

Two model species, *D. cingulatus* and *P. apterus,* were used for more detailed morphological and ontogenetic analysis. Specimens of both species were obtained from laboratory stock cultures. Besides cuticular color patterns, the epidermal were also examined in all stages of postembryonic development. The coloration of epidermis was either observed through a transparent non-melanized cutile (larvae of both species, adults of *D. cingulatus*), or the animals were beforehand dissected (adults of *P. apterus*).

Morphological analysis and statistical evaluation

The topological distribution of color spots over the abdominal segments was studied. Abdominal segments II to VII were chosen for study, since they are clearly visible and mainly uniform in shape. The abdominal surface was divided into a grid of 120 approximately square-like fields (Fig. 1A), in which the presence vs. absence of melanized cuticle (1 vs. 0) was recorded. An individual field was considered to be melanized if (a) it was completely melanized, or (b) it contained a small melanized spot (a "melanization centre") not exceeding the field borders, or (c) a large melanized spot originating outside the field covered more than 50% of its area. Data obtained by transformation of existing color patterns to the square grid (Fig. 1A) could be compared due to the similar body shapes of the examined species.

The transformed color patterns were tested statistically to reveal regularities in color pattern diversity within the examined taxa. Lygaeinae, Rhyparochrominae, Largidae, Pyrrhocoridae, and Phopalidae were analysed separately. To identify pairs of fields with parallel melanization, the concept of "conjunctions" was introduced. Fields ♯1 and ♯2 were in conjunction if ♯1 was melanized *just when* ♯2 was melanized. In other words, a conjunction displays a completely concerted melanization of two fields. The fields melanized in less than 10 percent of the examined species within each taxon were excluded from analysis.

The conjunctions fell into four categories: (A) metameric conjunctions between fields on the same (anterior or posterior) halves of different abdominal segments, (B) conjunctions between two fields on the same half of a single segment, (C) conjunctions between two fields on different halves of a single segment, and (D) conjunctions between fields on different halves of different segments (Fig. 1A). Since the number of all possible conjunctions differs for each category (3,000 for A and D, ·540 for B, 600 for C), direct comparison of the frequency of the individual categories of conjunctions was not possible. The observed numbers of the conjunctions (N_{obs}) were tested against the expected numbers of the conjunctions (N_{exp}, reflecting 3,000 : 540 : 600 : 3,000 ratio if the probability of all categories of conjunctions was equal) by χ^2 test. The null hypothesis that categories A+B (i.e., those revealing the "half-segment" arrangement) are equal to C+D was also tested by the χ^2 test (against 3,540:3,600 ratio).

Clonal analysis of mosaic epidermis

A laboratory stock of *mosaic* (*mo*) mutant of *P. apterus*, possibly transposon-mediated, was analysed [20, 26–27]. The epidermis of *mo* bugs displays an irregular mosaic of pigmented cells (red anterior, yellow posterior) with transparent (whitish) cell clones lacking pteridine pigments. The distribution of transparent cell clones was considered an apparent marker of normal behaviour of epidermal cell lineages, as the individuals of the *mo* strain do not differ from those of the wild-type in any fundamental morphological, developmental and ecophysiological features. Moreover, when *mo* insects are compared to X-ray-treated animals (for example, [11]), little or no incidence of extraordinary cell deaths should be expected.

Last-instar larvae, whose epidermis is well visible through a transparent cuticle and whose epidermal clones are the best-developed, were studied. Only abdominal segments IV-VI were analysed (both dorsal and ventral surfaces). Since the extent of transparent clones varies considerably in the *mo* strain, only specimens with distinct, sharply outlined patches were anlaysed. Each abdominal segment consists of two distinctly colored areas, red (approximately on the anterior two thirds of the segment) and yellow (the posterior third). A grid of six parallel transversal lines (A, R_1, R_2, RY, Y, P) was superimposed over the segment so that two lines (A, P) fitted the intersegmental boundaries, one (RY) fitted the boundary between the red and yellow parts of the segment, two (R_1, R_2) were laid on the red area, and one (Y) on the yellow area (see Fig. 1B). The distribution pattern of the cell clones was quantified as the number of the patches crossed by the grid lines (see camera lucida drawing in Fig. 1B).

Several hundreds of bugs of both sexes were used for basic screening, and those with suitably distinct clones (10 males, 10 females) were selected for a detailed morphological analysis, which was made on more than 400 uncolored patches.

RESULTS

Development of color patterns in the model species

Postembryonic development of abdominal coloration in *D. cingulatus* and *P. apterus* is summa-

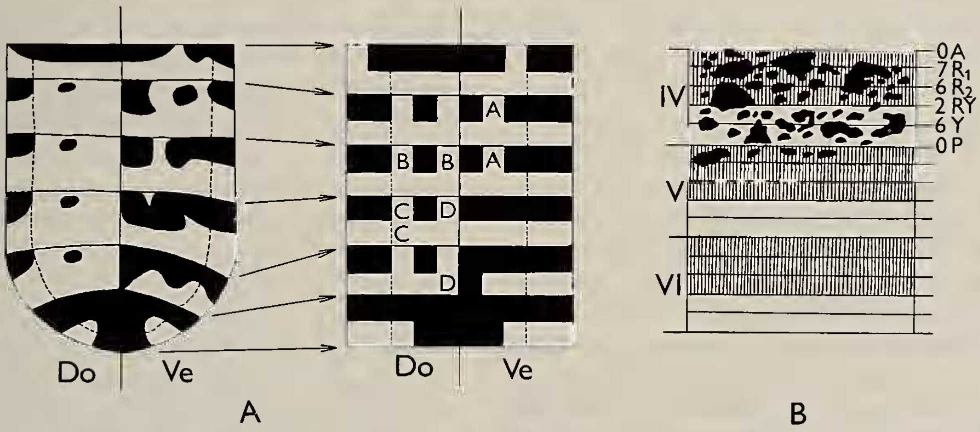

FIG. 1A. A method for transformating the color pattern into grid form (exemplified by *Spilostethus saxatilis* [Lygaeidae]). Do: dorsal, Ve: ventral surface; A-D: categories of conjunctions (A: conjunctions between fields on the same halves of different abdominal segments, B: conjunctions between two fields on the same half of a single one segment, C: conjunctions between two fields on different halves of a single segment, D: conjunctions between fields on different halves of different segments).

FIG. 1B. A method of evaluation of the transparent clones (black) in *mo* mutant of *P. apterus*. IV-VI: abdominal segments; dashed areas: red epidermis; open areas: yellow epidermis; A, R_1, R_2, RY, Y, P: arbitrary grid lines (A, P: intersegmental boundaries; RY: boundary between the red and yellow parts of the segment; R_1, R_2: red area; Y: yellow area); 0, 7, 6, 2, 6, 0: numbers of the clones crossed by the grid lines (in camera lucida drawing).

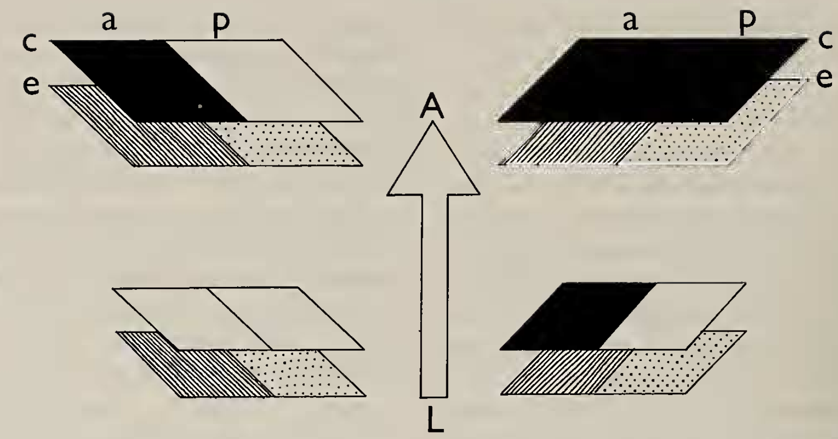

Fig. 2. Postembryonic development of abdominal color patterns in *D. cingulatus* (left) and *P. apterus* (right). L: larvae; A: adults; a: anterior part of a segment; p: posterior part of a segment; c: cuticle; e: epidermis; black areas: melanized cuticle; open areas: transparent cuticle; dashed areas: red epidermis; dotted areas: white or yellow epidermis.

rized in Figure 2. Both species show epidermal color patterns in addition to the cuticular ones. Whereas the epidermis is red or orange-red in the anterior parts of segments, it is either white (*D. cingulatus,* ventral side) or yellow (*P. apterus,* around the entire body) in the posterior parts of segments in both larvae and adults. Posterior boundaries of cuticular melanization in adult *D. cingulatus* completely coincide with the boundaries between red and white epidermal cells (Fig. 2). Similarly, the cuticular melanized spots, which are still distinct in the larvae of *P. apterus,* never reach over the epidermal boundaries from the red to the yellow regions (Fig. 2).

A similar epidermal coloration was previously described by Lawrence [11–12] and Lawrence and Green [15] in *Oncopeltus fasciatus* (Lygaeidae: Lygaeinae). Undoubtedly this subdivision of segment epidermis is widespread among coreoid bugs, especially among the Pyrrhocoridae (Zrzavý, in prep.). In conclusion, cuticular and epidermal color patterns are highly congruent in the model species. A cuticular spot established in one half of a segment usually does not exceed its intersegmental as well as intrasegmental boundaries. The line dividing the segment into anterior and posterior parts (marked by different coloration of the epidermis of the model species) plays an important role in the anterior-posterior arrangement of cuticular coloration.

Clonal restriction in epidermal color pattern formation

As shown in Table 1, no clones seem to lie on the intersegmental boundaries in *P. apterus*; but any intrasegmental line is not an insurmountable barrier.

The red-yellow boundary appears to be the least exceedable, compared to the other lines. We are aware that our simple morphological method is not fully objective since not only the clones but also

Table 1. Distribution of colorless epidermal clones on the abdomen of *mo* mutant of *P. apterus* (10 males, 10 females; c. 7 patches per a segment in average). IV, V, VI: abdominal segments; A, R_1, R_2, RY, Y, P: arbitrary grid lines (A: anterior boundary of a segment; P: posterior boundary of it; R_1, R_2: two lines within the red region of a segment; RY: red/yellow intrasegmental boundary; Y: a line within the yellow region of a segment; see Fig. 1B); +: some number of clones might be overlooked

	A	R_1	R_2	RY	Y	P	Σ
IV	0	61	54	26	34+	1	176+
V	1	37	44	23	28+	0	133+
VI	0	37	31	21	17+	0	106+
Σ	1	135	129	70	79+	1	415+

TABLE 2. General pattern of color conjunctions in Lygaeinae, Pyrrhocoridae and Rhopalidae N_{obs}: total observed number of conjunctions within a taxon; N_{exp}:expected number of conjunctions if the probability of all categories is equal (3,000:540:600:3,000 ratio—see Material and Methods); A, B, C, D: categories of conjunctions (Fig. 1A); χ^2 test—**, ***: significant on the levels of probability $P=0.010$, and 0.001, respectively

	Lygaeinae (34 spp.)		Pyrrhocoridae (57 spp.)		Rhopalidae (17 spp.)	
	N_{obs}	N_{exp}	N_{obs}	N_{exp}	N_{obs}	N_{exp}
A	41	33.2	79	68.9	46	37.0
B	14	6.0	25	12.4	11	6.7
C	6	6.6	20	13.8	15	7.4
D	18	33.2	40	68.9	16	37.0
A+B	55	39.2	104	81.3	57	43.7
C+D	24	39.8	60	82.7	31	44.4
A:B:C:D	***		***		***	
(A+B):(C+D)	***		***		**	

their fragments could be enumerated, while very small transparent (i.e., whitish) clones on the yellow background may be overlooked. Hence, the number of clones within the yellow area (as well as the depth of "RY depression") may have been slightly underestimated.

General organization of color patterns in the coreoid bugs

The color arrangement in the coreoid families is obviously non-random, but organized according to the anterior-posterior polarity of each segment in Lygaeinae (Lygaeidae), Pyrrhocoridae, and Rhopalidae. A significant majority of the color-pattern conjunctions connects either fields lying on the same (anterior or posterior) halves of different segments, or fields lying on the same half of a single segment. Thus, from the four possible categories of conjunctions (see Material and Methods), those marked A and B clearly predominate. On the contrary, the C-category conjunctions connecting fields of the opposite halves of the same segment are less frequent. This data indicates an obviously metameric "half-segment" organization of abdominal color patterns in the taxa studied here (Table 2).

However, the dorsal parts of the abdomen (i.e., those covered by wings in resting position) reveal this metameric color pattern to a much lesser extent. This is because there is, particularly in Rhopalidae, a strong tendency of the abdominal dorsum to display another type of coloration, associated with the aposematic function during flight.

No general metameric arrangement is developed in the Rhyparochrominae (Lygaeidae) and Largidae.

DISCUSSION

Phylogenetic status of the metameric color patterns

Three coreoid taxa examined (Lygaeinae, Pyrrhocoridae, Rhopalidae) apparently tend to generate very similar metameric arrangements of the color pattern. However, each differs from others in some details. For example, the lateral sectors ("connexiva") of both Lygaeinae and Rhopalidae display a clear metamerism, but while the melanized spots usually appear on the anterior halves of the segments in Lygaeinae, they are found on the posterior in Rhopalidae.

It can be assumed that the lygaeines, pyrrhocorids, and rhopalids do not constitute a monophyletic taxon, rather that they represent independent phylogenetic lines of the coreoid bugs. Thus, although our knowledge of phylogenetic relationships among the coreoid bugs is rather scant

[24, 29], and, further, the evolution of their color patterns has never been rigorously analysed, the hypothesis of the homology of their color patterns should be rejected [32]. The majority of the coreoid bugs has cryptic coloration without any conspicuous patterns on the abdominal segments. It appears that the wasp-like abdominal color pattern results from aposematic function of the coloration, which certainly does not belong to the coreoid groundplan. For example, the Rhyparochrominae (a group cladistically related to Pyrrhocoridae, Largidae, Rhopalidae and some other families) and the Largidae (a pyrrhocorid sister group) show complex (but generally cryptic) pyrrhocorid-like color patterns on the pronotum and forewings and generally uniform coloration of abdomen [32].

In conclusion, the wasp-like patterns undoubtedly are not homologous. Instead, the metameric color patterns seem to have arisen independently at least three times during the evolution of the Coreoidea s. lat.—(a) in Lygaeinae, (b) in Pyrrhocoridae, and (c) in Rhopalidae [32]. Yet in spite of the undoubtedly polyphyletic origin of the "wasp-like" color patterns in the Coreoidea s. lat., their diversity is strongly constrained to the formation of a single general organization of color fields, with iteration of the "half-segment" units.

Morphogenetic nature of the color patterns metamerism

The results acquired by clonal analysis of the abdominal epidermis in *P. apterus* are quite compatible with those of Lawrence [11–13] and Lawrence and Green [15]. They showed by clonal analysis of the abdominal epidermis of *O. fasciatus* that (a) segment epidermis is of a polyclonal nature and epidermal cell lineages do not cross intersegmental boundaries; (b) although many clones are sufficiently large to span the entire segment length, no clone comprises both the anterior and posterior margins of the same segment; (c) clones are usually laterally elongated; and (d) clones usually do not cross the intrasegmental boundary between bands of red and white epidermis. Concluding, regions of red and white (or yellow) epidermis in the bugs seem to represent further morphogenetic units within the abdominal segments, and they may represent relatively independent cell lineages (Fig. 3; see Table 1).

These conclusions can, moreover, be applied as well to cuticular color spots of coreoid bugs, which are laterally arranged and do not span the segment

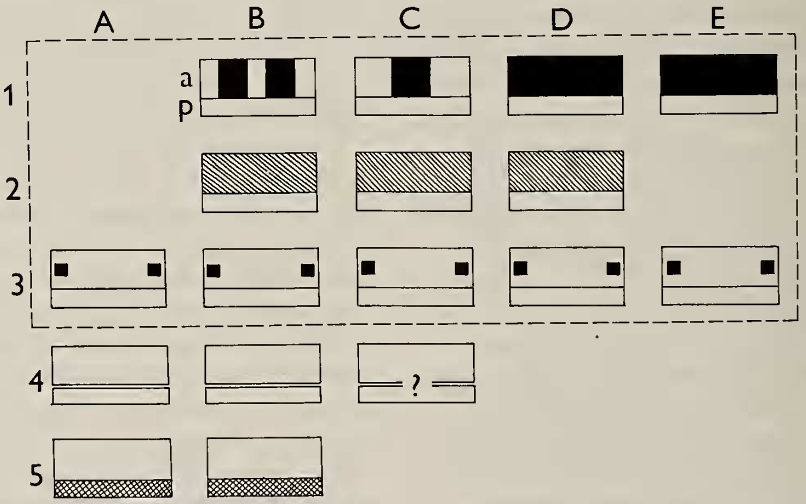

Fig. 3. Comparison of body compartmentalization of the *Drosophila* and coreoid bugs. A: *Drosophila*; B: *O. fasciatus*; C: *P. apterus*; D: *D. cingulatus*; E. coreoid bugs in general; 1: cuticular coloration (orig.); 2: epidermal coloration ([2, 11–13, 15], orig.); 3: position of a spiracle ([7], orig.); 4: clonal restriction [6, 11–16, orig.]; 5: *engrailed* expression pattern [2, 7, 14], a: anterior compartment; p: posterior compartment. Markers available for comparative morphological analysis are boxed.

length. Both color patterns, epidermal and cuticular, seem to be organized with respect to the same line, the "red-white boundary", and the evolution of the aposematic wasp-like coloration only further reveals this basic two-fold organization of the abdominal segment.

This intrasegmental boundary coincides with the line least exceedable by cell lineages, that is, with the possible intrasegmental compartmental boundary, analogous to that of *Drosophila* (Fig. 3) [1, 6–10, 14, 16–18, 25, 30]. The integument of each body segment of *Drosophila* is derived from two cell polyclones, the anterior and posterior compartments, each of which is characterized by a unique combination of active selector genes, and therefore forms a distinct component of the pattern. The compartment seems to be a functional unit for subsequent patterning (including also color-pattern formation: for example, the anterior compartments are melanized, the posterior ones non-melanized).

Using an antibody binding to the product of the segmentation gene *engrailed* (*en*), Campbell and Caveney [2] have shown that *en*-positive cells in *O. fasciatus* form a continuous band localized immediately anterior to the segment border. This pattern of *en* expression is identical to that of posterior compartments in *Drosophila* [7, 9–10, 14], as well as other flies [28], bees [4–5] and locusts [22], and even the crustaceans [22] and centipedes [31]. The size and location of the *en*-positive cell band of the *O. fasciatus* corresponds precisely to a distinct band of white-pigmented epidermal cells [2]. In other words, white pigmentation of the epidermis is a conspicuous morphological marker of the posterior compartment (Fig. 3).

Conclusions

(A) The red-yellow intrasegmental boundary in *P. apterus* seems to display clonal properties similar to the red-white boundary in *O. fasciatus,* and is probably homologous to it (Figs. 3B-C).

(B) The intrasegmental transversal line, marked by contrasting epidermal coloration in the model species, shares the basic properties of the intrasegmental compartment boundary of *Drosophila* segments, and is probably homologous to it (Figs. 3A-C).

(C) The red-yellow boundary takes a considerable role in cuticular color-pattern formation, being hardly exceedable by the cuticular spots established in one half of the segment (Fig. 3).

(D) The great majority of the cuticular color patterns, although independently evolved, respects the same organization scheme. This diversity can be thus regarded as constrained by the compartment boundaries, both inter- and intrasegmental. The uniform organizational scheme of abdominal color patterns in the coreoid bugs seems to serve as a good morphological marker of body compartmentalization.

Consequently, the coreoid bugs can provide a good model for comparative studies of body metamerism, since their compartmentalization seems to be distinctly marked by wild-type body coloration in a large number of species. There is surely some factual bridge between *Drosophila* developmental biology and comparative insect morphology, however careful one must be in making such generalizations.

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